

RESEARCH ARTICLE

Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail

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ABSTRACT

Birds in subtropical deserts face significant thermoregulatory challenges because environmental temperatures regularly exceed avian body temperature. To understand the differing susceptibility of desert birds to increasing temperatures, we examined thermoregulatory performance and estimated heat tolerance limits (HTLs) for three Sonoran Desert nesting bird species – Gambel's quail, mourning doves and white-winged doves. Using flow-through respirometry we measured daytime resting metabolism, evaporative water loss and real-time body temperature at air temperatures (T_{air}) from 30°C to 66°C. We found marked increases in resting metabolism at the upper critical temperature (T_{uc}), which was significantly lower in the quail ($T_{\text{air}}=41.1^\circ\text{C}$) than in both dove species ($T_{\text{air}}=45.9\text{--}46.5^\circ\text{C}$). Gambel's quail maintained low resting metabolic rates and low rates of evaporative water loss at their T_{uc} (0.71 W and 1.20 g H₂O h⁻¹, respectively), but were more sensitive to increasing air temperature, reaching their HTL at T_{air} of 52°C. Mourning doves and white-winged doves maintained low resting metabolic rates (0.66 and 0.94 W), but higher rates of evaporative water loss (1.91 and 2.99 g H₂O h⁻¹) at their T_{uc} and reached their HTL at T_{air} of 58–60°C. Mass-specific evaporative water loss in white-winged doves (147 g) and mourning doves (104 g) was 45% and 30% greater, respectively, than the rate observed in Gambel's quail (161 g) at T_{air} of 48°C. Higher rates of evaporation and higher T_{uc} made the doves exceptionally heat tolerant, allowing them to maintain body temperatures at least 14°C below air temperatures as high as 60°C (140°F).

KEY WORDS: Evaporative water loss, Resting metabolic rate, Upper critical temperature, Body temperature, Thermoregulation, Heat tolerance limit

INTRODUCTION

Birds in hot environments face significant physiological challenges when environmental temperatures exceed body temperature, a situation where evaporation is the only avenue for heat dissipation (Calder and King, 1974). Increasing air temperatures drive increases in avian body temperature, metabolism and evaporative water loss in an effort to offset increasing heat loads, but the costs incurred can affect survival and fitness (McKechnie and Wolf, 2010; Cunningham et al., 2013a,b). Warmer and more frequent hot days over land are virtually certain by the late 21st century (IPCC, 2013) and will be accompanied by hotter, longer and more frequent heat waves (Meehl and Tebaldi, 2004; IPCC, 2011; Rahmstorf and Coumou, 2011).

These rapid increases in environmental temperatures over the coming century will increasingly tax the abilities of animals to thermoregulate effectively and may dramatically influence community structure and the distribution of animals (McKechnie et al., 2012; Diffenbaugh and Field, 2013; Quintero and Wiens, 2013).

The high solar heat loads and high air temperatures of the world's deserts already routinely expose birds to environmental or operative environmental temperatures (T_e) that greatly exceed avian body temperature (Bakken, 1976; Robinson et al., 1976). Gambel's quail (*Callipepla gambelii* Gambel 1843) foraging on a typical hot summer day in the Sonoran Desert, for example, experience T_e approaching 50°C (Goldstein, 1984). Desert-nesting doves often place their nests in sites with high solar heat loads, where the nest environment can reach T_e of 50–60°C, which demands that incubating birds cool their eggs to maintain viable egg temperatures (B.O.W., personal observation; Russell, 1969; Walsberg and Voss-Roberts, 1983; Marder and Gavrieli-Levin, 1986).

Despite decades of research on thermoregulation in birds, our information on the thermoregulatory performance of wild birds exposed to air temperatures above body temperature is limited. Early research on avian thermoregulation in the heat focused on passerines, which evaporate water from their respiratory surfaces by panting (Dawson and Bartholomew, 1968). Heat loss through panting is an active process, requiring muscular movement of the respiratory apparatus, a metabolically costly effort that produces heat. Rates of water loss through panting are very high and in small passerines may exceed 5% of body mass per hour (Wolf and Walsberg, 1996). A lack of sweat glands and the thick plumage were thought to impede significant evaporation from the skin in birds (Calder and Schmidt-Nielsen, 1967). Smith and Suthers (1969) showed that pigeons and doves dissipate large heat loads by cutaneous evaporation with little increase in metabolism, allowing rock doves (*Columba livia*) to raise young at air temperatures as high as 60°C (Marder and Arieli, 1988). The strong reliance on cutaneous evaporation in the heat is apparently widespread in columbiform birds, where it has been observed in two of this study's species – mourning doves (*Zenaida macroura* Linnaeus 1758) and white-winged doves (*Zenaida asiatica* Linnaeus 1758) (Hoffman and Walsberg, 1999; McKechnie and Wolf, 2004) – but not in galliform birds (Marder, 1983; Marder and Ben-Asher, 1983). Other mechanisms that enhance evaporative heat loss such as gular flutter, deep esophageal pulsation and cloacal evaporation remain poorly understood (Calder and King, 1974; Gaunt, 1980; Dawson, 1982; Baumel et al., 1983; Schleucher et al., 1991; Hoffman et al., 2007).

Among the modest number of studies that have examined heat tolerance of birds, differences in methodologies make it difficult to draw broad conclusions. These studies often relied on birds raised or held in captivity for long periods at standard temperatures (e.g. 25–30°C; see Hudson and Brush, 1964; Lasiewski and Seymour,

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List of symbols and abbreviations

BMR	basal metabolic rate (W)
EHL	whole animal evaporative heat loss rate (W)
EHL/MHP	evaporative cooling capacity
EWL	whole animal evaporative water loss rate ($\text{g H}_2\text{O h}^{-1}$)
HTL	heat tolerance limit ($^{\circ}\text{C}$)
M_b	initial body mass (g)
MHP	whole animal metabolic heat production (=RMR)
RMR	whole animal resting metabolic rate (W)
T_{air}	chamber air temperature ($^{\circ}\text{C}$)
T_b	body temperature ($^{\circ}\text{C}$)
T_e	operative environmental temperature ($^{\circ}\text{C}$)
T_{uc}	upper critical temperature ($^{\circ}\text{C}$)

1972; Weathers, 1981; Hoffman and Walsberg, 1999; Hoffman et al., 2007). Because heat-acclimated birds can tolerate significantly higher temperatures than birds acclimated to lower standard temperatures (Marder and Arieli, 1988; McKechnie and Wolf, 2004), prior heat stress studies may have greatly overestimated the susceptibility of subjects to elevated temperatures.

Here, we present data on the thermoregulatory performance of the Gambel's quail, a galliform, and two species of columbiforms, the mourning dove and white-winged dove, with the aim of quantifying responses to heat stress in birds summer-acclimatized to a hot subtropical desert. We continuously measured body temperature (T_b , $^{\circ}\text{C}$), whole animal rates of evaporative water loss (EWL, $\text{g H}_2\text{O h}^{-1}$) and daytime resting metabolism (RMR, W) in response to chamber air temperature (T_{air} , ranging from 30°C to 66°C) in birds on the day they were captured. We hypothesized that like rock doves, white-winged doves and mourning doves would demonstrate high tolerances for heat, and nearly constant T_b and RMR with increasing T_{air} . Because galliforms lack the cutaneous evaporative cooling of columbiforms, we anticipated that Gambel's quail would demonstrate lower tolerances for heat and show more rapid increases in T_b and RMR with increasing T_{air} . We present these species together because of their ecological similarities as large (>100 g), desert-nesting granivores with overlapping distributions, but make no inferences about adaptive differences. Thus, we examine their relative thermoregulatory performance without having a sufficient number of species to consider their evolutionary histories (Garland et al., 1992, 1993, 2005; Blomberg et al., 2003).

MATERIALS AND METHODS**Site description**

Birds were captured in June and July of 2012 (white-winged and mourning doves) and in July of 2013 (Gambel's quail) in northwest Tucson, Arizona, USA. Experiments were conducted on the same day as capture. During June and July of 2012, temperatures at the Tucson AZMET weather station ranged from 14 to 42°C , daily maximum temperatures ranged from 31 to 42°C and the dew point ranged from -15 to 22°C . During July of 2013, temperatures ranged from 21 to 41°C , daily maximum temperatures ranged from 32 to 41°C , and the dew point ranged from 7 to 23°C .

Animal capture and handling

The birds were captured using standard walk-in traps baited with seed and held outdoors in shaded, darkened screen cages [model 1450B, 12" (30.5 cm) cubed, BioQuip, Rancho Dominguez, CA, USA]. None of the birds received supplemental food after capture. However, they probably continued digesting seed in their crops and were not post-absorptive; thus, we assumed for metabolic measurements an RER of 1 and $20.9 \text{ J ml}^{-1} \text{ CO}_2$ produced (Gessaman and Nagy, 1988; Walsberg and Wolf, 1995). Free water was provided to the quail but they were not observed to drink. Thus, prior to each experimental run, the quail were provided between 3 and 6 ml of tap water via

oral gavage. Five white-winged doves were also given additional water by gavage prior to high-temperature runs and no differences in thermal tolerance were observed compared to un-watered individuals. Prior to each experimental run, a temperature-sensitive PIT (passive integrated transponder) tag (model TX1411BBT, Biomark, Boise, ID, USA) was injected into each bird's abdominal cavity. Use and accuracy of these tags for T_b measurement is detailed in Whitfield et al. (2015). Following experimental runs, where birds were exposed to high temperatures, birds were placed in front of cool air flow and T_b was monitored until it returned to resting levels ($\sim 40^{\circ}\text{C}$); Gambel's quail were also gavaged with tap water post-exposure to ensure rehydration. Birds were monitored for 1–5 h after exposure, after which the doves were released at the site of the experiments and quail from their site of capture. Animal care protocols were approved by the Institutional Animal Care and Use Committee of the University of New Mexico (protocol no. 12-100537-MCC). Birds were captured under permits from the US Fish and Wildlife Service and the Arizona Game and Fish Department.

Measurements of resting metabolism and evaporative water loss

Measurements of RMR and EWL were made using a flow-through respirometry system similar to Whitfield et al. (2015). The respirometry chamber consisted of a transparent plastic container (5 litre, 22 cm \times 25 cm \times 12 cm, Rubbermaid, Atlanta, GA, USA) sealed with an opaque lid, modified by addition of inlet and outlet ports, and containing a plastic mesh platform above a 2 cm layer of medium weight mineral oil to trap excreta. The chamber was placed inside a modified ice chest where temperature was controlled to $\pm 0.5^{\circ}\text{C}$. Mass-flow controllers (Alicat, Tucson, AZ, USA) provided dry air to the chamber from a pump through columns of silica gel and drierite connected in series (2012) or from a compressor through a membrane dryer (2013: Champion[®] CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA). Excurrent air was sampled at 250 ml min^{-1} and directed to a $\text{CO}_2/\text{H}_2\text{O}$ gas analyzer (model LI-840A, LICOR, Lincoln, NE, USA). Gas analyzer outputs were sampled once per second by Expedata (version 1.4.15, Sable Systems, Las Vegas, NV, USA).

Following PIT tag insertion, a bird was weighed (model V31XH2, accuracy=0.1 g, Ohaus, Parsippany, NJ, USA) and placed in the darkened respirometry chamber, where an infrared light and video camera enabled continuous viewing. The bird was exposed to one or more thermoneutral temperatures (30 or 35°C) and one or more higher temperatures (40 – 66°C in 2°C increments) in a stepped pattern of temperature trials over the span of the 1–3 h experimental run. In order to keep H_2O content of the respirometry chamber at values that would not impede evaporation (dew point $< 5^{\circ}\text{C}$), flow rates were maintained between 5 and $40 \text{ litre min}^{-1}$ depending on T_{air} and the bird's evaporative rate. The initial thermoneutral temperature trial allowed a bird to calm from handling; H_2O and CO_2 production were monitored and observed to drop to resting levels (typically within 30 min). T_{air} was then increased to higher trial temperatures and birds were allowed to adjust to each temperature for 10–20 min and stabilize before moving to the next temperature. Most birds remained calmer when flow rates were higher and chamber humidity was lower (< 5 ppt water vapor).

As T_{air} was increased above thermoneutrality, T_b and activity were monitored closely to prevent mortality. A trial was ended and the bird recorded as reaching its thermal limit if it: (1) remained continuously active for 5–10 min, (2) showed a T_b approaching or exceeding 45°C , or (3) showed a loss of balance or righting response (extremely rare). In some trials, birds were exposed to T_{air} levels that were at or near their thermal limits, but these measurements were not designed to elicit mortality. Unlike critical thermal maxima trials where mortality is common (reviewed in Lutterschmidt and Hutchison, 1997), our procedure resulted in rates of mortality of less than 1%. In addition, the experimental runs were timed to end before a bird had lost more than 10% of M_b during a trial (including any fecal losses). Approximately 5 min of baseline data were collected following each temperature trial.

Data analysis

We selected the lowest 1 min (doves) or 5 min (quail) average of CO_2 ppm readings less baseline values for each trial temperature. Birds noted as active or failing or having mean $T_b > 44.7^{\circ}\text{C}$ or slope of $T_b > 0.1^{\circ}\text{C min}^{-1}$ during a temperature trial were not included in the analysis. Using eqn 10.5 of

Lighton (2008), we estimated the rate of CO₂ production in ml CO₂ min⁻¹ and whole-animal RMR in watts (W), assuming an RER of 1 (see Animal capture and handling). Rates of whole-animal EWL (g H₂O h⁻¹) were calculated from the H₂O ppt readings (less baseline values) for the same data points using eqn 10.9 of Lighton (2008).

Statistical analysis

Statistical analyses and graphs were produced using R (v3.1; R Development Core Team, 2011) inside RStudio (v0.98.932). We used the linear mixed effects model from the nlme package and individual as a random factor (Pinheiro et al., 2014) due to the repeated measurement of individuals in an unbalanced design. We used the segmented package (Muggeo, 2008) to determine inflection points in the metabolic data. The main effects examined in all analysis were T_{air} and species. M_b was used as a covariate in all analysis. Backwards-stepwise model selection was used where the initial model included all covariates, random factors and main effects, including two-way interactions between main effects.

RESULTS

Body mass

Initial body mass (M_b) averaged 160.7±11.1 g (mean±s.d.; $N=19$) for Gambel's quail, 104.0±10.2 g ($N=49$) for mourning doves and 147.3±17.7 g ($N=52$) for white-winged doves (Table 1). M_b ($P<0.001$), species ($P=0.002$) and T_{air} ($P<0.001$) all significantly predicted RMR and EWL in the species tested.

Resting metabolism among species

A significant relationship between RMR and body mass was found among species ($F_{1,107}=52.1$, $P<0.001$). Thus, mass-independent RMR residuals were calculated to investigate the mass-independent responses to air temperature among species (Packard and Boardman, 1999). Segmented regressions of these RMR residuals against air temperature allowed us to identify inflection points of 41.1°C in Gambel's quail, 45.9°C in mourning doves and 46.5°C in white-winged doves (Fig. S1). These inflection points represent the upper critical temperatures (T_{uc}) above which daytime RMR increases sharply (Kendeigh, 1969; Table 1). The 95% CI of these T_{uc} values overlapped considerably between the two dove species, did not overlap between Gambel's quail and mourning doves, and slightly overlapped between Gambel's quail and white-winged doves – the upper bound of the former being 43.1°C and the lower bound of the latter being 42.8°C (Table 1). A z -score comparing the mean T_{uc} values of Gambel's quail and white-winged doves nonetheless revealed their significant difference ($z=2.55$; $P<0.01$). Thus, while T_{uc} values did not differ among dove species, T_{uc} values for Gambel's quail were significantly lower than those for both dove species.

Resting metabolism

For T_{air} between 30°C and the T_{uc} , RMR decreased as T_{air} increased ($F_{1,44}=24.3$, $P<0.001$), but this response differed among species

($F_{1,88}=21.9$, $P<0.001$) and was significantly influenced by M_b ($F_{1,88}=30.8$, $P<0.001$). Above the T_{uc} , RMR increased as T_{air} increased ($F_{1,65}=43.4$, $P<0.001$); this response also differed among species ($F_{1,92}=11.3$, $P=0.001$) and was significantly influenced by M_b ($F_{1,92}=48.1$, $P<0.001$). Thus, the effects of T_{air} and M_b were assessed for each species independently.

For Gambel's quail exposed to T_{air} below their T_{uc} of 41.1°C, RMR decreased with increasing T_{air} ($F_{1,5}=15.5$, $P<0.05$; Fig. 1) but was unaffected by M_b ($F_{1,15}=0.04$, $P=0.85$). RMR increased with T_{air} above the T_{uc} ($F_{1,11}=24.6$, $P<0.001$; Fig. 1) with a slope of 0.022 W °C⁻¹ (Table 2), and M_b was a significant covariate ($F_{1,16}=8.03$, $P<0.05$). RMR was lowest at the T_{uc} and averaged 0.71 W or 4.55 mW g⁻¹ (Table 1) and RMR averaged 0.75 W at T_{air} of 42°C and 0.79 W at 48°C (Table 3).

For mourning doves at T_{air} below their T_{uc} of 45.9°C, RMR decreased with increasing T_{air} ($F_{1,16}=10.1$, $P<0.01$; Fig. 1) and M_b was a significant covariate ($F_{1,40}=8.42$, $P<0.01$). RMR increased with T_{air} above the T_{uc} ($F_{1,27}=22.3$, $P<0.001$; Fig. 1) with a slope of 0.017 W °C⁻¹ (Table 2) and M_b was a significant covariate ($F_{1,37}=9.66$, $P<0.01$). RMR averaged 0.64 W at T_{air} of 42°C, 0.66 W or 6.07 mW g⁻¹ at the T_{uc} and 0.58 W at 48°C (Tables 1 and 3).

For white-winged doves at T_{air} below their T_{uc} of 46.5°C, RMR decreased with increasing T_{air} ($F_{1,21}=7.18$, $P<0.05$; Fig. 1) and M_b was a significant covariate ($F_{1,30}=18.8$, $P<0.001$). RMR increased with T_{air} above the T_{uc} ($F_{1,25}=12.3$, $P<0.01$; Fig. 1) with a slope of 0.019 W °C⁻¹ (Table 2) and M_b was a significant covariate ($F_{1,36}=5.73$, $P<0.05$). RMR averaged 0.99 W at T_{air} of 42°C, 0.94 W or 6.49 mW g⁻¹ at the T_{uc} , and 0.97 W at 48°C (Tables 1 and 3).

Evaporative water loss

For T_{air} below the T_{uc} , there was a significant effect of T_{air} ($F_{1,43}=197.9$, $P<0.001$), species ($F_{1,88}=28.0$, $P<0.001$), and M_b ($F_{1,88}=32.2$, $P<0.001$) – as well as a significant interaction of T_{air} and species ($F_{1,43}=22.2$, $P<0.001$) – on EWL (g H₂O h⁻¹) indicating differences in the slope of this relationship among species. For T_{air} above the T_{uc} , EWL was significantly affected by T_{air} ($F_{1,64}=475.6$, $P<0.001$), species ($F_{1,92}=28.8$, $P<0.001$), M_b ($F_{1,92}=67.9$, $P<0.001$) and an interaction of T_{air} and species ($F_{1,64}=30.8$, $P<0.001$). Thus, there was a significant difference in the response of EWL to T_{air} among species both above and below the respective T_{uc} .

For Gambel's quail at T_{air} below their T_{uc} of 41.1°C, EWL increased with T_{air} ($F_{1,5}=20.1$, $P<0.01$; Fig. 2) with a slope of 0.035 g H₂O h⁻¹ °C⁻¹ (Table 2) but was unaffected by M_b ($F_{1,15}=0.00$, $P=0.98$). EWL increased more steeply with T_{air} above the T_{uc} ($F_{1,11}=176.3$, $P<0.001$); 0.196 g H₂O h⁻¹ °C⁻¹; Fig. 2; Table 2). EWL averaged 0.67 g H₂O h⁻¹ at T_{air} of 35°C, 1.71 g H₂O h⁻¹ at 42°C and 2.46 g H₂O h⁻¹ at 48°C (Table 3).

Table 1. Mean±s.d. values for variables measured in three Sonoran Desert nesting bird species

Species	Body mass (g)	Normothermic T_b (°C) ^a	T_{uc} (°C)	RMR (W) ^b	RMR (mW g ⁻¹) ^b	EWL (g H ₂ O h ⁻¹) ^b	HTL (°C)	T_b (°C) ^c	EHL/MHP ^c
Gambel's quail	160.7±11.1 ($N=19$)	41.1±0.5	41.1	0.71±0.09	4.55±0.63	1.20±0.43	52	43.6±0.8	2.14±0.30
Mourning dove	104.0±10.2 ($N=49$)	41.0±0.8	45.9	0.66±0.10	6.07±0.72	1.91±0.21	58	41.9±0.9	3.08±0.48
White-winged dove	147.3±17.7 ($N=52$)	41.4±0.6	46.5	0.94±0.29	6.49±1.78	2.99±0.66	60	42.7±0.9	3.69±1.24

^a $T_{\text{air}} \leq 39^\circ\text{C}$. Sample sizes (n) ranged between 11 and 16.

^b $T_{\text{air}} (\pm 1^\circ\text{C}) = T_{\text{uc}}$ (upper critical temperature). Sample sizes (n) ranged between 7 and 15.

^c $T_{\text{air}} (\pm 1^\circ\text{C}) = \text{HTL}$ (heat tolerance limit) -2°C . Sample sizes (n) ranged between 5 and 6.

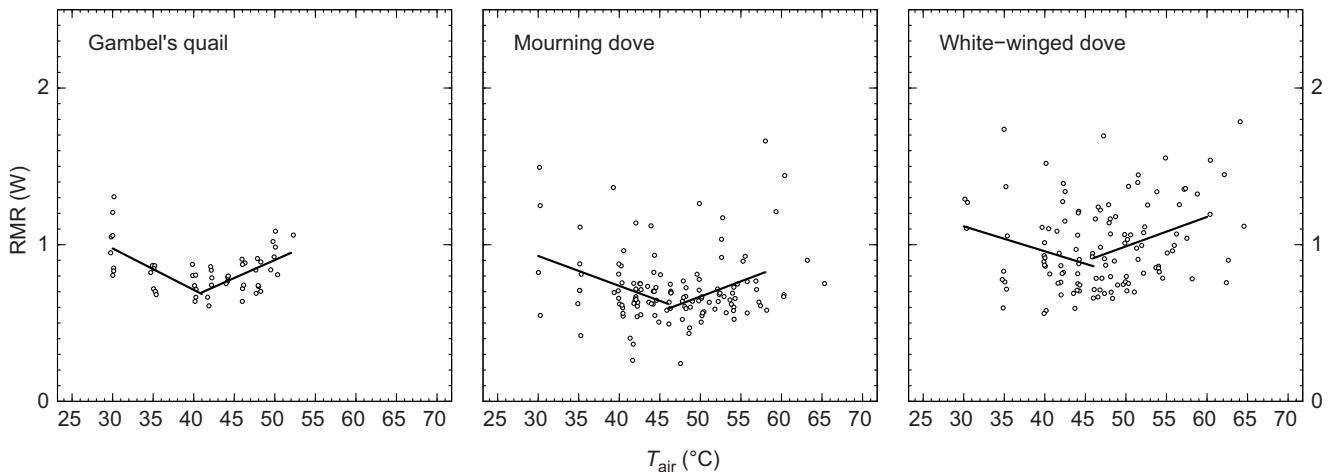


Fig. 1. Resting metabolic rate as a function of air temperature in Gambel's quail, mourning doves and white-winged doves. RMR was regressed against T_{air} below (all $P < 0.05$) and above the T_{uc} (all $P < 0.01$). T_{uc} in Gambel's quail, mourning doves and white-winged doves are 41.1, 45.9 and 46.5°C, respectively. See text for statistical details of linear regressions, Table 2 for parameter estimates and Fig. S1 for determination of T_{uc} using RMR residuals.

For mourning doves at T_{air} below their T_{uc} of 45.9°C, EWL increased with T_{air} ($F_{1,16}=63.6$, $P < 0.001$; Fig. 2) with a slope of 0.069 g H₂O h⁻¹ °C⁻¹ (Table 2) and M_b was a significant covariate ($F_{1,40}=14.2$, $P < 0.001$). EWL increased more steeply with T_{air} above the T_{uc} ($F_{1,27}=286.2$, $P < 0.001$; 0.210 g H₂O h⁻¹ °C⁻¹; Fig. 2; Table 2) and M_b was a significant covariate ($F_{1,37}=11.6$, $P < 0.01$). EWL averaged 0.74 g H₂O h⁻¹ at T_{air} of 35°C, 1.27 g H₂O h⁻¹ at 42°C and 1.96 g H₂O h⁻¹ at 48°C (Table 3).

For white-winged doves at T_{air} below their T_{uc} of 46.5°C, EWL increased with T_{air} ($F_{1,21}=87.9$, $P < 0.001$; Fig. 2) with a slope of 0.140 g H₂O h⁻¹ °C⁻¹ (Table 2) and M_b was a significant covariate ($F_{1,30}=12.9$, $P < 0.01$). EWL increased more steeply with T_{air} above the T_{uc} ($F_{1,25}=174.5$, $P < 0.001$; 0.383 g H₂O h⁻¹ °C⁻¹; Fig. 2; Table 2). EWL averaged 0.99 g H₂O h⁻¹ at T_{air} of 35°C, 1.95 g H₂O h⁻¹ at 42°C and 3.41 g H₂O h⁻¹ at 48°C (Table 3).

Ratio of evaporative heat loss to metabolic heat production

We converted EWL to rates of whole-animal evaporative heat loss (EHL, W) using a latent heat of vaporization of water of 2.26 J (mg H₂O)⁻¹ and define the ratio EHL/MHP – a dimensionless metric for evaporative cooling capacity – as EHL relative to metabolic heat production (MHP=RMR). For T_{air} below the T_{uc} , there was a significant effect of T_{air} ($F_{1,43}=374.7$, $P < 0.001$) and species ($F_{1,89}=6.50$, $P < 0.05$), as well as a significant interaction of T_{air} and species ($F_{1,43}=14.9$, $P < 0.001$) on EHL/MHP. For T_{air} above the

T_{uc} , EHL/MHP showed a significant effect of T_{air} ($F_{1,64}=282.6$, $P < 0.001$) and species ($F_{1,93}=6.01$, $P < 0.05$) and a significant interaction of T_{air} and species ($F_{1,64}=10.6$, $P < 0.01$). Thus, there was a significant difference in the response to T_{air} among species both above and below the respective T_{uc} . There were no significant effects of M_b on EHL/MHP ($P > 0.05$), either above or below the T_{uc} .

In Gambel's quail EHL/MHP increased with T_{air} both below and above the T_{uc} (below: $F_{1,5}=57.4$, $P < 0.001$; above: $F_{1,11}=33.9$, $P < 0.001$; Fig. 3). EHL/MHP averaged 0.55 at T_{air} of 35°C, 1.42 at 42°C and 1.97 at 48°C, increasing 3.6-fold between 35 and 48°C (Table 3). At T_{air} of 50°C, just below the HTL (heat tolerance limit, see below), Gambel's quail reached a maximum EHL/MHP of 2.14 (Table 1).

In mourning doves EHL/MHP increased with T_{air} both below and above the T_{uc} (below: $F_{1,16}=123.8$, $P < 0.001$; above: $F_{1,27}=159.1$, $P < 0.001$; Fig. 3). EHL/MHP averaged 0.65 at T_{air} of 35°C, 1.26 at 42°C and 2.19 at 48°C, increasing 3.4-fold between 35 and 48°C (Table 3). At T_{air} of 56°C, just below the HTL, mourning doves reached a maximum EHL/MHP of 3.08 (Table 1).

In white-winged doves EHL/MHP increased with T_{air} both below and above the T_{uc} (below: $F_{1,21}=122.9$, $P < 0.001$; above: $F_{1,25}=84.5$, $P < 0.001$; Fig. 3). EHL/MHP averaged 0.62 at T_{air} of 35°C, 1.22 at 42°C and 2.27 at 48°C, increasing 3.7-fold between 35 and 48°C (Table 3). At T_{air} of 58°C, just below the HTL, white-winged doves reached a maximum EHL/MHP of 3.69 (Table 1).

Table 2. Slope (m) and intercept (b) for the relationships of metabolic variables in response to air temperature (T_{air}) below and above the upper critical temperature (T_{uc}) in Gambel's quail, mourning doves and white-winged doves

Species	T_{uc}	Regression	m	b	Regression	m	b
Gambel's quail	41.09	RMR ($\leq T_{\text{uc}}$)	-0.026 (-0.039, -0.013)	1.76 (1.29, 2.22)	RMR ($> T_{\text{uc}}$)	0.022 (0.013, 0.032)	-0.21 (-0.66, 0.24)
Mourning dove	45.89	RMR ($\leq T_{\text{uc}}$)	-0.019 (-0.031, -0.007)	1.49 (0.99, 1.99)	RMR ($> T_{\text{uc}}$)	0.017 (0.010, 0.025)	-0.15 (-0.54, 0.25)
White-winged dove	46.47	RMR ($\leq T_{\text{uc}}$)	-0.011 (-0.020, -0.003)	1.41 (1.05, 1.78)	RMR ($> T_{\text{uc}}$)	0.019 (0.008, 0.030)	0.04 (-0.53, 0.60)
Gambel's quail	41.09	EWL ($\leq T_{\text{uc}}$)	0.035 (0.019, 0.050)	-0.44 (-0.99, 0.11)	EWL ($> T_{\text{uc}}$)	0.196 (0.166, 0.225)	-6.75 (-8.14, -5.36)
Mourning dove	45.89	EWL ($\leq T_{\text{uc}}$)	0.069 (0.051, 0.087)	-1.54 (-2.29, -0.79)	EWL ($> T_{\text{uc}}$)	0.210 (0.184, 0.236)	-7.89 (-9.26, -6.53)
White-winged dove	46.47	EWL ($\leq T_{\text{uc}}$)	0.140 (0.112, 0.169)	-3.83 (-5.02, -2.64)	EWL ($> T_{\text{uc}}$)	0.383 (0.325, 0.441)	-15.19 (-18.21, -12.16)
Gambel's quail	41.09	EHL/MHP ($\leq T_{\text{uc}}$)	0.042 (0.031, 0.054)	-0.88 (-1.28, -0.49)	EHL/MHP ($> T_{\text{uc}}$)	0.095 (0.062, 0.127)	-2.59 (-4.11, -1.07)
Mourning dove	45.89	EHL/MHP ($\leq T_{\text{uc}}$)	0.082 (0.067, 0.096)	-2.16 (-2.76, -1.56)	EHL/MHP ($> T_{\text{uc}}$)	0.135 (0.113, 0.156)	-4.45 (-5.57, -3.33)
White-winged dove	46.47	EHL/MHP ($\leq T_{\text{uc}}$)	0.104 (0.085, 0.122)	-2.96 (-3.73, -2.19)	EHL/MHP ($> T_{\text{uc}}$)	0.176 (0.137, 0.214)	-6.20 (-8.20, -4.21)
Gambel's quail	-	-	-	-	T_b ($T_{\text{air}} > 39^\circ\text{C}$)	0.170 (0.129, 0.211)	34.61 (32.72, 36.50)
Mourning dove	-	-	-	-	T_b ($T_{\text{air}} > 39^\circ\text{C}$)	0.041 (0.028, 0.053)	40.24 (39.61, 40.88)
White-winged dove	-	-	-	-	T_b ($T_{\text{air}} > 39^\circ\text{C}$)	0.056 (0.034, 0.079)	39.32 (38.22, 40.42)

Values are means, with 95% confidence intervals in parentheses. Regressions of body temperature (T_b) are in response to air temperature (T_{air}) above 39°C.

Table 3. Mean±s.d. values for metabolic variables in Gambel's quail, mourning doves and white-winged doves at three air temperatures ($T_{\text{air}}\pm 1^\circ\text{C}$)

T_{air} ($^\circ\text{C}$)	Gambel's quail			Mourning dove			White-winged dove		
	35 $^\circ\text{C}$ (n=8)	42 $^\circ\text{C}$ (n=6)	48 $^\circ\text{C}$ (n=7)	35 $^\circ\text{C}$ (n=7)	42 $^\circ\text{C}$ (n=19)	48 $^\circ\text{C}$ (n=12)	35 $^\circ\text{C}$ (n=8)	42 $^\circ\text{C}$ (n=12)	48 $^\circ\text{C}$ (n=15)
RMR (W)	0.78±0.08	0.75±0.10	0.79±0.09	0.75±0.22	0.64±0.18	0.58±0.14	0.98±0.39	0.99±0.25	0.97±0.28
RMR (mW g^{-1})	4.77±0.58	4.50±0.46	5.00±0.54	7.37±2.32	6.32±1.71	6.11±1.72	6.90±1.81	6.76±1.54	6.57±1.70
EWL ($\text{g H}_2\text{O h}^{-1}$)	0.67±0.15	1.71±0.37	2.46±0.37	0.74±0.16	1.27±0.44	1.96±0.42	0.99±0.49	1.95±0.72	3.41±0.85
EWL (% of Mb h^{-1})	0.42±0.09	1.03±0.22	1.57±0.25	0.72±0.12	1.24±0.36	2.05±0.40	0.69±0.23	1.32±0.47	2.31±0.51
EHL/MHP	0.55±0.11	1.42±0.22	1.97±0.31	0.65±0.19	1.26±0.25	2.19±0.47	0.62±0.12	1.22±0.28	2.27±0.47
T_b ($^\circ\text{C}$)	41.1±0.6	41.8±0.6	42.5±0.8	41.0±0.7	42.0±0.5	42.1±0.8	41.3±0.6	41.9±0.7	41.7±0.9

Body temperature

For T_{air} below 39 $^\circ\text{C}$ there were no significant effects of M_b , species, T_{air} or the interaction of T_{air} and species on T_b ($P>0.05$) and thus T_b in this range were considered normothermic. For T_{air} above 39 $^\circ\text{C}$, however, T_b increased with T_{air} differentially among species (T_{air} : $F_{1,148}=79.2$, $P<0.001$; species: $F_{1,107}=4.9$, $P<0.05$; $T_{\text{air}}\times\text{species}$: $F_{1,148}=4.9$, $P<0.05$). Thus, above T_{air} of 39 $^\circ\text{C}$, there was a significant difference in the response of T_b to T_{air} among species.

T_{air} below 39 $^\circ\text{C}$ did not affect T_b in Gambel's quail ($F_{1,14}=0.08$, $P=0.78$) and normothermic T_b averaged 41.1 $^\circ\text{C}$ (Table 1). T_b increased with T_{air} above 39 $^\circ\text{C}$ ($F_{1,17}=67.8$, $P<0.001$; Fig. 4) with a fairly steep slope of 0.170 $^\circ\text{C }^\circ\text{C}^{-1}$ (Table 2). T_b averaged 41.8 and 42.5 $^\circ\text{C}$ at T_{air} of 42 and 48 $^\circ\text{C}$, respectively (Table 3) and 43.6 $^\circ\text{C}$ at T_{air} of 50 $^\circ\text{C}$ (Table 1). Thus at T_{air} of 50 $^\circ\text{C}$, just below the HTL, Gambel's quail maintained a T_a-T_b gradient of 6.4 $^\circ\text{C}$.

T_{air} below 39 $^\circ\text{C}$ did not affect T_b in mourning doves ($F_{1,9}=0.01$, $P=0.93$) and normothermic T_b averaged 41.0 $^\circ\text{C}$ (Table 1). T_b increased with T_{air} above 39 $^\circ\text{C}$ ($F_{1,68}=42$, $P<0.001$; Fig. 4) with a fairly shallow slope of 0.041 $^\circ\text{C }^\circ\text{C}^{-1}$ (Table 2). T_b averaged 42.0 and 42.1 $^\circ\text{C}$ at T_{air} of 42 and 48 $^\circ\text{C}$, respectively (Table 3) and 41.9 $^\circ\text{C}$ at T_{air} of 56 $^\circ\text{C}$ (Table 1). Thus at T_{air} of 56 $^\circ\text{C}$, just below the HTL, mourning doves maintained a T_a-T_b gradient of 14.1 $^\circ\text{C}$.

T_{air} below 39 $^\circ\text{C}$ did not affect T_b in white-winged doves ($F_{1,9}=0.40$, $P=0.54$) and normothermic T_b averaged 41.4 $^\circ\text{C}$ (Table 1). T_b increased with T_{air} above 39 $^\circ\text{C}$ ($F_{1,62}=25$, $P<0.001$; Fig. 4) with a fairly shallow slope of 0.056 $^\circ\text{C }^\circ\text{C}^{-1}$ (Table 2). T_b averaged 41.9 and 41.7 $^\circ\text{C}$ at T_{air} of 42 and 48 $^\circ\text{C}$, respectively (Table 3) and 42.7 $^\circ\text{C}$ at T_{air} of 58 $^\circ\text{C}$ (Table 1). Thus, at T_{air} of 58 $^\circ\text{C}$, just below the HTL, white-winged doves maintained a T_a-T_b gradient of 15.3 $^\circ\text{C}$.

Heat tolerance limit

The results presented thus far pertained to data collected from birds that were inactive and maintaining stable T_b (see Materials and methods). To investigate heat tolerance, we examined the final 5 min of all temperature trials above 39 $^\circ\text{C}$ with regard to T_b maximum and T_b slope (Fig. 5). The T_b (maximum, slope) for Gambel's quail (45.1 $^\circ\text{C}$, 0.27 $^\circ\text{C min}^{-1}$) and mourning doves (46.1 $^\circ\text{C}$, 0.24 $^\circ\text{C min}^{-1}$) resulted from individuals in 52 and 54 $^\circ\text{C}$ temperature trials, respectively; the values for white-winged doves (46.0 $^\circ\text{C}$, 0.39 $^\circ\text{C min}^{-1}$) were recorded by different individuals in trials of 54 $^\circ\text{C}$ and above. Individual birds passed a given trial if T_b and slope of T_b remained less than or equal to 44.7 $^\circ\text{C}$ and 0.1 $^\circ\text{C min}^{-1}$, respectively; individuals that exceeded either of these limits were classified as failing, indicating that the heat load experienced by an individual exceeded its thermoregulatory capacity and it had reached its heat tolerance limit (HTL). Once the majority of individuals failed in a trial at a given T_{air} , a species was considered to have reached its HTL. Thus, the HTL of Gambel's quail was 52 $^\circ\text{C}$ (1/9 pass), of mourning doves was 58 $^\circ\text{C}$ (3/8 pass) and of white-winged doves was 60 $^\circ\text{C}$ (1/4 pass; Fig. 5; Table 1).

DISCUSSION

In this study, we examined the thermoregulatory ability of wild doves and quail under conditions that normally persist during the summer in hot subtropical deserts. We maintained low chamber humidities (dew point <5 $^\circ\text{C}$) to maximize the evaporative gradient and used summer-acclimatized birds in order to make measurements under ecologically relevant conditions. White-winged and mourning doves demonstrated a heat tolerance and ability to thermoregulate at T_{air} as high as 60 $^\circ\text{C}$, while Gambel's quail did so successfully up to 50 $^\circ\text{C}$.

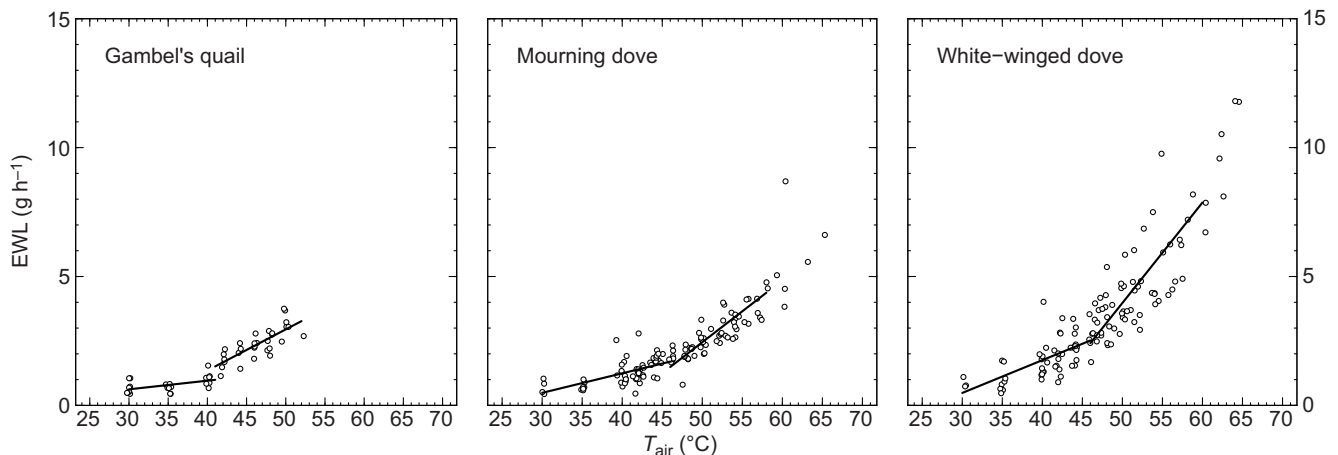


Fig. 2. Rate of evaporative water loss as a function of air temperature in Gambel's quail, mourning doves and white-winged doves. EWL was regressed against T_{air} below (all $P<0.01$) and above the T_{uc} (all $P<0.001$). T_{uc} in Gambel's quail, mourning doves and white-winged doves are 41.1, 45.9 and 46.5 $^\circ\text{C}$, respectively. See text for statistical details of linear regressions, Table 2 for parameter estimates and Fig. S1 for determination of T_{uc} using RMR residuals.

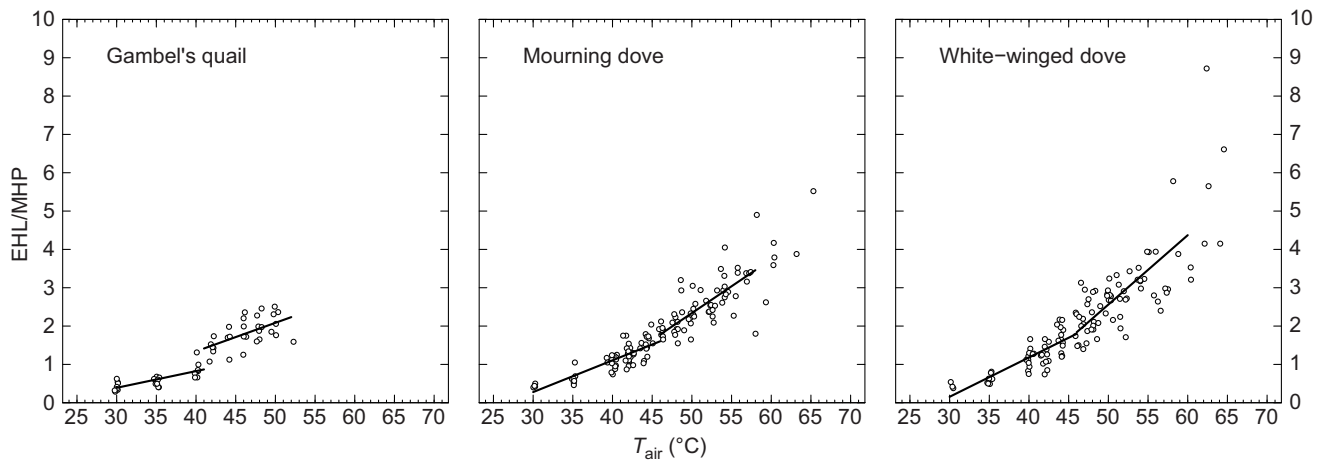


Fig. 3. Evaporative cooling capacity (EHL/MHP) as a function of air temperature in Gambel's quail, mourning doves and white-winged doves. EHL/MHP was regressed against T_{air} below and above the T_{uc} (all $P < 0.001$). T_{uc} in Gambel's quail, mourning doves and white-winged doves are 41.1, 45.9 and 46.5°C, respectively. See text for statistical details of linear regressions, Table 2 for parameter estimates, and Fig. S1 for determination of T_{uc} using RMR residuals.

Earlier studies often did not provide conditions conducive for examining natural responses to heat stress. Hudson and Brush (1964), for example, found that mourning doves died at T_{air} above 41°C and that California quail (*Callipepla californica*) could not survive T_{air} above 44°C. Birds exposed to very high environmental temperatures in nature are typically subject to very low atmospheric humidity. High chamber humidity impeded the birds' ability to evaporate water and severely limited their ability to cope with heat stress (see Lasiewski et al., 1966, and Whitfield et al., 2015, for more discussion of these issues).

In addition, most studies of thermoregulation in these taxa have focused on responses to T_{air} below normothermic T_{b} . Prior to this study, thermoregulatory performance at T_{air} above 40°C had only been quantified in 9 of the 300+ species of columbiform birds and 7 of the 170+ species of galliform birds (see Figs 6 and 7). Of these, only 4 columbiform and 3 galliform species were exposed to T_{air} above 45°C. Below, we discuss the thermoregulatory performance of each study species in detail and compare our observations to earlier relevant studies in galliform and columbiform birds as well as speculate on their future performance in a warmer and dryer environment.

Resting metabolism and upper critical temperature

Understanding changes in RMR with changes in T_{air} is critical to quantifying thermoregulatory capacity in the heat. We found similar slopes in doves and quail for changes in RMR and mass independent RMR at T_{air} above the T_{uc} (Table 2, Table S1). However, the $T_{\text{uc}} - T_{\text{air}}$ at which heat dissipation becomes an active process and marked increases in daytime RMR occur (Kendeigh, 1969) – was significantly lower in the quail (41.1°C) than observed in both dove species (45.9–46.5°C) (Table 1). These differences in the T_{uc} among doves and quail are importantly related to pathways of evaporative heat dissipation. At a T_{air} of 30°C, evaporative losses in most birds are more or less evenly distributed between respiratory and cutaneous pathways (Bernstein, 1971; Ro and Williams, 2010). At a $T_{\text{air}} \geq 40^\circ\text{C}$, the primary evaporative pathway is respiratory in passerines ($\geq 75\%$, Wolf and Walsberg, 1996) and galliforms (75%, Richards, 1976) and cutaneous in doves ($\geq 70\%$, McKechnie and Wolf, 2004). Since metabolic heat contributes to total heat load, birds that actively dissipate heat via panting (quail, passerines) tend to have lower limits of heat tolerance and relatively high rates of water loss compared with doves, which dissipate most of their heat load using cutaneous evaporation.

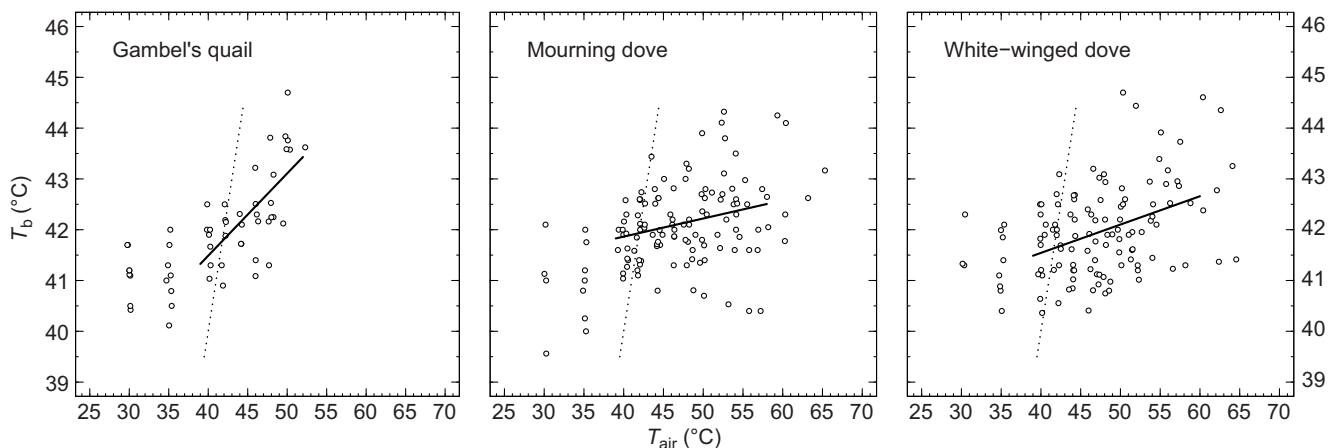


Fig. 4. Body temperature as a function of air temperature in Gambel's quail, mourning doves and white-winged doves. Body temperature was regressed against air temperature above 39°C (all $P < 0.001$). See text for statistical details of linear regressions and Table 2 for parameter estimates. The dotted lines represent $T_{\text{b}} = T_{\text{air}}$.

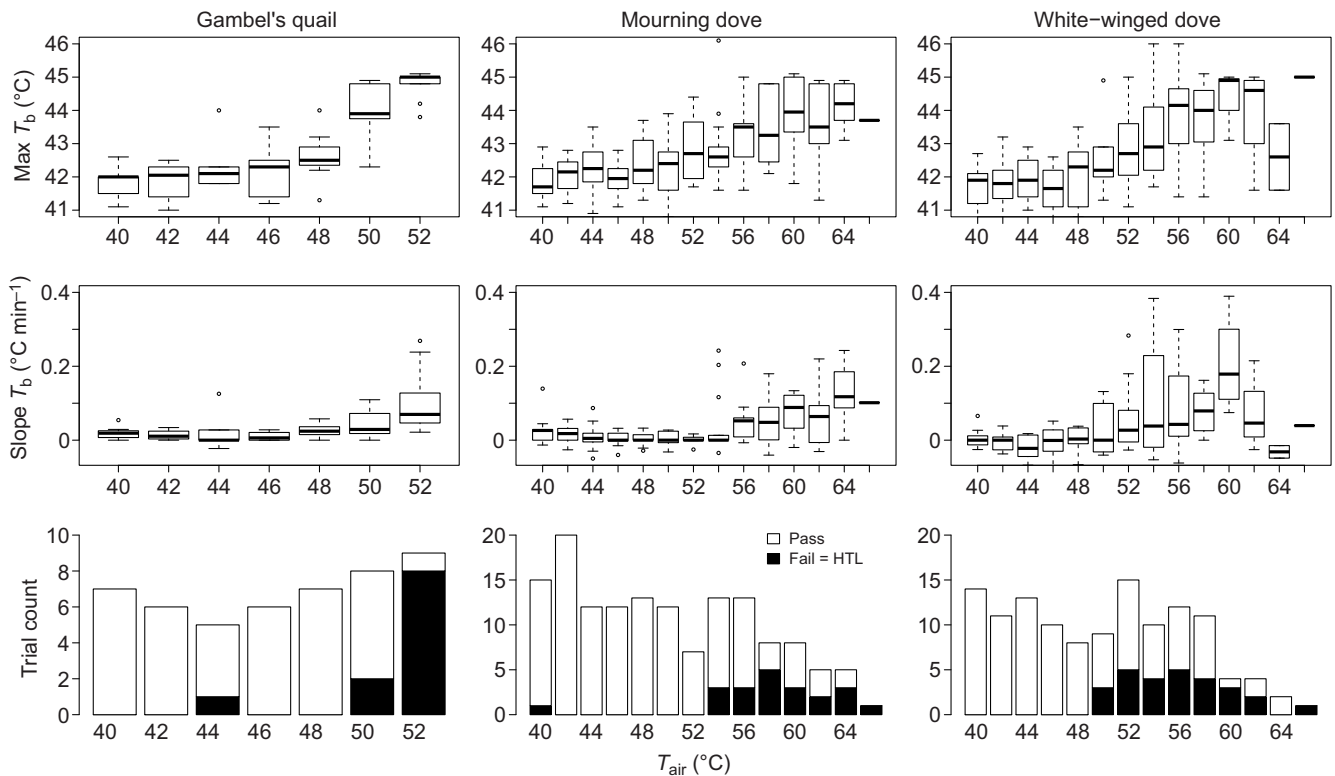


Fig. 5. Maximum body temperature and slope of body temperature during temperature trials at air temperatures $\geq 40^{\circ}\text{C}$ in Gambel's quail, mourning doves and white-winged doves. In temperature trials, a bird passed until reaching its heat tolerance limit (fail=HTL, coded in black), when maximum body temperature exceeded 44.7°C or slope of body temperature exceeded $0.1^{\circ}\text{C min}^{-1}$ during the last 5 min of a trial.

Other studies of columbiforms have reported responses of metabolic rate to temperature similar to those reported in the current study (Fig. 6). In rock doves acclimated to very high T_{air} (up to 62°C) metabolic rate remained constant from 30 to 60°C and no T_{uc} is apparent (Marder and Arieli, 1988). White-winged doves acclimated to 43°C showed no significant difference in RMR between 35 and 45°C (McKechnie and Wolf, 2004), but these T_{air} were below the T_{uc} found in this study. Spinifex Pigeons (89 g, *Geophaps plumifera*; Withers and Williams, 1990) and Crested Pigeons (186 g, *Ocyphaps lophotes*; B.O.W., unpublished results), like the two species of dove tested here, show T_{uc} of 46°C . However, three columbiforms, including the diamond dove (~ 40 g, *Geopelia*

cuneata), crested pigeon (174 g) and brush bronzewing (224 g, *Phaps elegans*), show T_{uc} close to normothermic T_{b} , which is contrary to the pattern we observed and may be due to acclimation history or measurement dates or conditions (Schleucher, 1999; Larcombe et al., 2003). In each of these cases, the experimental birds were housed outdoors at T_{air} below 25°C , suggesting a seasonal adjustment of T_{uc} like that of BMR (McKechnie, 2008). Given their capacities for cutaneous heat dissipation, doves in the wild may only rarely experience heat loads that require panting and an increase in RMR.

Galliform birds such as quail, pheasants and partridges, in contrast, show clear well-defined T_{uc} where metabolic rate increases

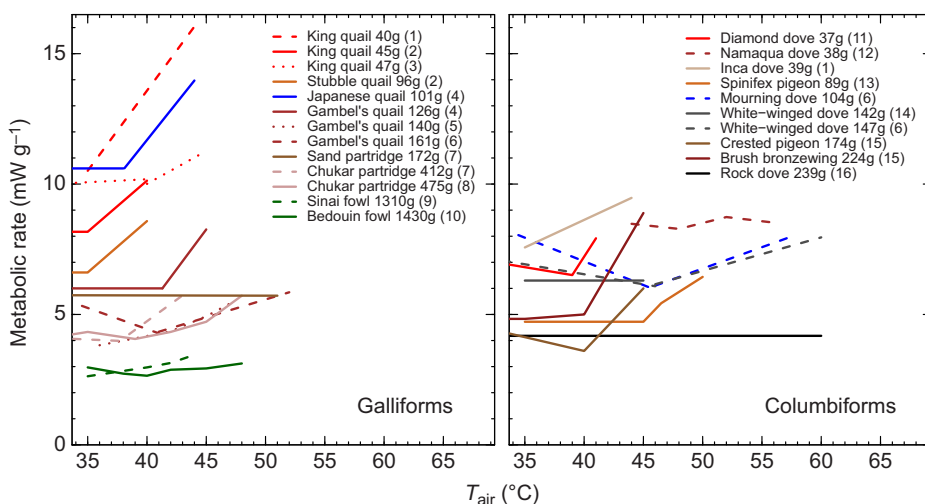


Fig. 6. Metabolic rate as a function of air temperature in galliform and columbiform birds. Data obtained from a range of authors: ¹Lasiewski and Seymour, 1972; ²Roberts and Baudinette, 1986; ³Pis, 2010; ⁴Weathers, 1981; ⁵Goldstein and Nagy, 1985 (data from summer of 1981); ⁶This study; ⁷Frumkin et al., 1986; ⁸Marder and Bernstein, 1983; ⁹Arad and Marder, 1982; ¹⁰Marder, 1973; ¹¹Schleucher, 1999; ¹²Gerson et al., 2014; ¹³Withers and Williams, 1990; ¹⁴McKechnie and Wolf, 2004; ¹⁵Larcombe et al., 2003; ¹⁶Marder and Arieli, 1988.

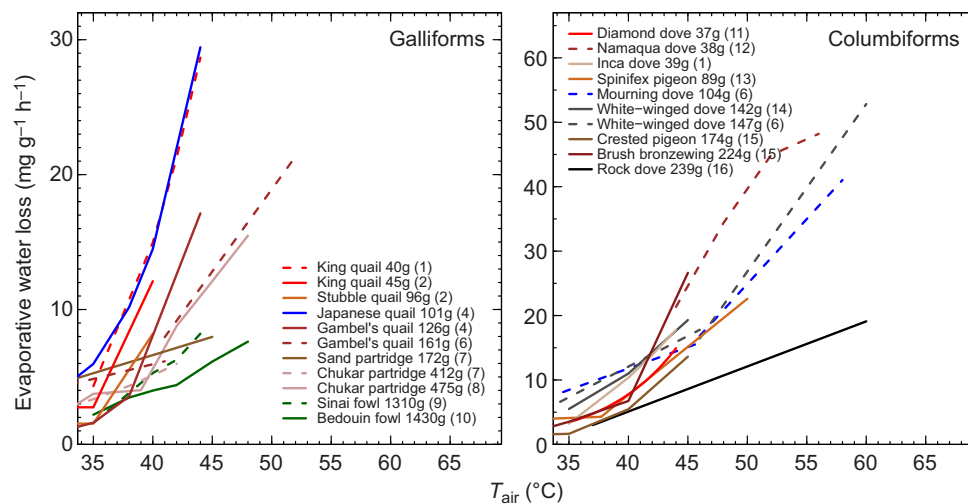


Fig. 7. Rate of evaporative water loss as a function of air temperature in galliform and columbiform birds. Note difference in scale of ordinate between the two graphs. Numbers refer to references as listed in Fig. 6.

markedly with increasing heat stress. T_{uc} values for galliforms in the heat tend to cluster around normothermic T_b and show only modest variability (Fig. 6). Data from eight studies encompassing six species show that T_{uc} range from 35 to 42°C with only the sand partridge (*Ammoperdix heyi*) showing no increase in metabolic rate with T_{air} ranging from 35 to 50°C. Sand partridges, thus, appear more similar to columbiform birds in that their metabolic rate does not increase steeply at any point (Frumkin et al., 1986), which suggests that an elaborated gular mechanism or enhanced cutaneous evaporation may occur in this species. Our T_{uc} value for Gambel's quail is similar to other studies for the same species (Goldstein and Nagy, 1985; Weathers, 1981), indicating that T_{uc} in galliform birds tends to fall just below or slightly above T_b .

Given the differences in individual birds, their acclimation history, the time of year and experimental conditions, the lowest metabolic rates we measured are similar to previous measurements of RMR and BMR in these species. For Gambel's quail in this study, RMR was 4.6 mW g⁻¹ at the T_{uc} (Table 1), which is less than the BMR of 6.0 mW g⁻¹ found for birds acclimated to 25°C (Weathers, 1981) and comparable with an RMR of 5.0±1.7 mW g⁻¹ ($n=24$; 33°C≤ T_{air} ≤47°C) found in wild birds – as in this study – acclimatized to the Sonoran Desert summer (Goldstein and Nagy, 1985). For mourning doves in this study, RMR was 6.1 mW g⁻¹ at the T_{uc} , which is less than the BMR of 7.1 mW g⁻¹ observed in birds at higher humidities and acclimated to 25°C (Hudson and Brush, 1964; appendix A of McNab, 2009). For white-winged doves in this study, RMR was 6.5 mW g⁻¹ at the T_{uc} , which compares favorably with the metabolic rate (6.3±0.8 mW g⁻¹; $n=15$; 35°C≤ T_{air} ≤45°C) found for birds acclimated to 43°C (McKechnie and Wolf, 2004).

Evaporative water loss

Gambel's quail showed a significant increase in EWL at the T_{uc} of 41.1°C (Table 2, Fig. 2). The marked increase in RMR and EWL together indicate an increase in respiratory evaporation at a T_{air} coinciding with their normothermic T_b . Doves also increased EWL at their T_{uc} , but this value was ~46°C. Their reliance on cutaneous evaporation, which has negligible metabolic costs (Marder and Ben-Asher, 1983; Marder and Gavrieli-Levin, 1987), allowed these doves to defer active heat dissipation via panting and/or gular flutter to a T_{air} approximately 5°C higher than normothermic T_b .

Despite their differences in M_b , mourning doves and Gambel's quail showed similar responses of EWL above their respective T_{uc} (Table 2, Table S1). However, as a percentage of M_b , EWL was 30%

greater in mourning doves (2.1% M_b h⁻¹) and 45% greater in white-winged doves (2.3% M_b h⁻¹) than that observed in Gambel's quail (1.6% M_b h⁻¹) at a T_{air} of 48°C (Table 3). White-winged doves increased their EWL with T_{air} more steeply than the other two species, both above and below T_{uc} (Table 2, Table S1). Compared with similarly sized Gambel's quail, white-winged doves evaporated water at higher rates over a range of high T_{air} , which provided a greater cooling capacity, but resulted in greater rates of water loss.

Evaporative water loss generally scales with M_b with increasing T_{air} in both galliforms and columbiforms (Fig. 7). At the highest T_{air} measured among columbiforms, ~55–60°C, EWL ranges from 2–3% M_b h⁻¹ in rock doves to 4–5% M_b h⁻¹ in the smaller dove species (39–147 g). At the highest T_{air} frequently measured among galliforms, ~44–45°C, EWL ranges from 0.7% M_b h⁻¹ in the large bedouin fowl (~1400 g, *Gallus domesticus*) to 3% M_b h⁻¹ in the small king quail (40 g, *Coturnix chinensis*). In this study EWL in Gambel's quail at T_{air} of 50°C measured about 2% M_b h⁻¹.

Ratio of evaporative heat loss to metabolic heat production

At T_{air} just below their respective HTL we found that Gambel's quail are able to produce EHL/MHP of 2.14 at 50°C, with mourning doves producing ratios of 3.08 at 56°C and white-winged doves showing ratios of 3.69 at 58°C (Table 1). In prior studies, only the larger rock doves exhibit ratios approaching 3.0 at 60°C (Marder and Arieli, 1988). The smaller spinifex pigeons had EHL/MHP ratios of 1.25–1.5 at 45°C and 1.75 at 50°C (Dawson and Bennett, 1973; Withers and Williams, 1990). Data for small doves (~40 g) show that these species can produce EHL/MHP ratios of 1.0 (diamond dove), 1.1–1.2 (Inca dove, *Columbina inca*) and 1.6 (Namaqua dove, *Oena capensis*) at 44°C (Schleucher et al., 1991; Lasiewski and Seymour, 1972; MacMillen and Trost, 1967; Schleucher, 1999; Gerson et al., 2014). Among these smaller doves, the Namaqua doves appear to be more heat tolerant than the other smaller species, although this could be an artifact of acclimation or measurement conditions, producing EHL/MHP of 3.55 at 56°C (Gerson et al., 2014), which is comparable to the value we found for white-winged doves at 58°C. Overall, heat-acclimatized doves exposed to T_{air} of 55–60°C dissipate heat through evaporation at 3- to 3.7-fold their rates of metabolic heat production and thus are able to cope with extremely high environmental heat loads.

Excluding the Gambel's quail used in this study, galliforms ranging in size from 40 to 1400 g have not been shown to produce EHL/MHP ratios >2.0 or tolerate T_{air} above 48°C . Large Sinai and bedouin fowls (~ 1300 – 1400 g) produce a maximum EHL/MHP of 1.65 at 44°C and apparently tolerate maximum T_{air} of 48°C (Marder, 1973; Arad and Marder, 1982). Chukar partridge (475 g, *Alectoris chukar*) are able to produce EHL/MHP of 1.82 at 48°C and reached their heat tolerance limits in trials $>48^{\circ}\text{C}$ (see below; Marder and Bernstein, 1983). Japanese quail (~ 100 g, *Coturnix japonica*) produce a maximum EHL/MHP of 1.12 at a T_{air} of 43°C . The smallest galliform that has been studied, king quail (~ 40 g), produced a EHL/MHP ratio of 1.17 at 45.2°C (Lasiewski et al., 1966) and 1.23 at 44°C (Lasiewski and Seymour, 1972). In general, it appears that galliforms are able to tolerate maximum T_{air} of ~ 48 – 50°C and are able to evaporate water at rates that can account for slightly more than two times their RMR at the highest T_{air} .

Body temperature and heat tolerance limit

Facultative hyperthermia represents a means of partially offsetting heat gain in hot environments and reducing EWL and, as a consequence, is a well-developed response in heat stressed and exercising birds. We found that the normothermic T_{b} for mourning and white-winged doves averaged 41.0 and 41.4°C , respectively (Table 1). The T_{b} of both species increased linearly with T_{air} above this range, staying well below lethal temperatures and reaching a value of 41.9°C for T_{air} of 56°C in mourning doves and 42.7°C for T_{air} of 58°C in white-winged doves (Table 1). This increase of 0.9°C for mourning and 1.3°C for white-winged doves from normothermic T_{b} falls below the 1.6 to 4.2°C range of T_{b} increases found for other columbiform birds exposed to lower T_{air} of 44 – 45°C (Lasiewski and Seymour, 1972; MacMillen and Trost, 1967; Schleucher, 1999; Withers and Williams, 1990; Larcombe et al., 2003), although it exceeds the 0.8°C variation in T_{b} found for heat-acclimated rock doves exposed to T_{air} of 30 – 60°C (Marder and Arieli, 1988). At $\sim 41^{\circ}\text{C}$, the normothermic T_{b} of Gambel's quail and the dove species were very similar. As T_{air} increased, however, T_{b} of Gambel's quail had a significantly steeper slope and lower intercept than that of both dove species (Fig. 4, Table 2), reaching 43.6°C at T_{air} of 50°C (Table 1). Thus, just below the HTL, Gambel's quail maintained a $T_{\text{air}}-T_{\text{b}}$ gradient of just 6.4°C , compared with 14.1 and 15.3°C , respectively, for mourning and white-winged doves.

Establishing the thermal tolerance of animals to heat stress is a prerequisite for understanding how heat exposure and its severity may impact wild animal populations. Historically, these determinations have taken a variety of forms, but the assays typically produced high mortality in the subjects and most have tended to focus on ectotherms (98% of 604 animal taxa reviewed by Lutterschmidt and Hutchison, 1997). In this study, we measured core T_{b} continuously, rather than recording a single T_{b} measurement at the end of a temperature trial, which allowed us to determine both maximum T_{b} of individuals as well as the response of T_{b} to changes in T_{air} . Thus, we could determine real time if an individual had reached its thermal limits and terminate the trial without harming the bird. The HTL metric provided a clear T_{air} above which birds could not maintain a constant T_{b} . Using a protocol similar to ours, Marder and Bernstein (1983) found that chukar partridges exposed to T_{air} of 48°C maintained a stable T_{b} for 2–4.5 h, but could not maintain T_{b} below lethal levels at T_{air} of 52°C . Thus, like the quail observed in our study, this large galliform (475 g) reached its limit of heat tolerance at a T_{air} of 52°C . Our findings and those of others provide strong evidence that desert-dwelling columbiform birds, primarily

because of their high rates of cutaneous evaporation, cope better with high heat loads than galliforms in the same environment.

Ecological aspects of thermoregulatory performance in doves and quail

Williams et al. (2012) has suggested that desert birds need the capacity to increase EWL during periods of extreme heat in order to maintain sub-lethal T_{b} , while minimizing dehydration over the long term. In this study, we found that the thermoregulatory performance and water balance of mourning and white-winged doves differed greatly from that of the sympatric Gambel's quail. The quail showed lower RMR and lower mass-specific EWL at T_{air} above normothermic T_{b} , which serves to conserve water and energy, but also potentially makes them vulnerable to increasing temperatures, especially during heat waves. Doves, in contrast, support a high water use 'lifestyle' when environmental temperatures exceed normothermic T_{b} . Thus, at a T_{air} of 48°C , mourning and white-winged doves lose 10% M_{b} in water over a period of 4–5 h, while this takes 6 h or more in Gambel's quail. Greater rates of EWL in doves could reduce their abundance if water were unavailable, for example, because of longer or more intense droughts (IPCC, 2013; Albright et al., 2010); but it also allows them to survive at temperatures of 60°C or more. With their more constrained EWL and greater reliance on respiratory EWL, Gambel's quail appear to have heat tolerance limits that are significantly lower than those observed in doves – but may persist without water for longer periods in moderate heat.

The differing thermoregulatory responses among the three species to high T_{air} , in part, may reflect their differing ecologies within the Sonoran Desert. Mourning and white-winged doves often nest in exposed locations with significant solar heat loads, where the nest environment can reach T_{e} of 50 – 60°C and incubating birds must cool rather than warm their eggs to maintain viability (B.O.W., personal observation; Russell, 1969; Walsberg and Voss-Roberts, 1983). Doves require access to preformed water almost daily and travel up to 20 km or more access water holes (Gubanich, 1966; Brown, 1989); their strong flight capabilities allow them to nest many miles from water sources (Bartholomew and Dawson, 1954). In addition, doves are able to rapidly drink by suction, placing their bills in water sources and drinking continuously. Mourning doves deprived of water for 24 h can drink 17% of their M_{b} in water in 10 min (Bartholomew and Dawson, 1954). Gambel's quail are much less mobile and typically range about 0.5 km from their roost sites (Gorsuch, 1934). During the Sonoran Desert summer, they constrain their activities to shaded microsites during the heat of the day, with only intermittent exposure to the sun when moving between shaded sites or flying short distances (Goldstein, 1984; Goldstein and Nagy, 1985). Gambel's quail often live independent of surface water resources and rely on vegetation and insects in desert valleys far from water (Lowe, 1955; Hungerford, 1960; Bartholomew and Cade, 1963). Very high air temperatures, however, may constrain the ability of quail to forage and potentially limit their distribution in future climates (Goldstein, 1984; McKechnie and Wolf, 2010).

It is critical that we understand the thermoregulatory and water balance challenges that birds face in a rapidly warming world. Such understanding might allow us predict and perhaps mitigate such events; it is a prerequisite for understanding avian distributions now and in a warmer future. This study is a first step in examining the relative responses of birds to higher temperatures and gives us some baseline measure of their ecological performance. Given the apparent differences among species in physiological responses to

heat stress, examining the tolerances of naturally occurring avian communities in similar ways will be critical for understanding their composition and persistence.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

B.O.W. designed the study. B.O.W., E.K.S. and A.R.G. designed the experimental set up. E.K.S., J.O., A.R.G. and B.O.W. collected data. E.K.S. analyzed the data. E.K.S., A.R.G. and B.O.W. wrote the manuscript.

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Supplementary information

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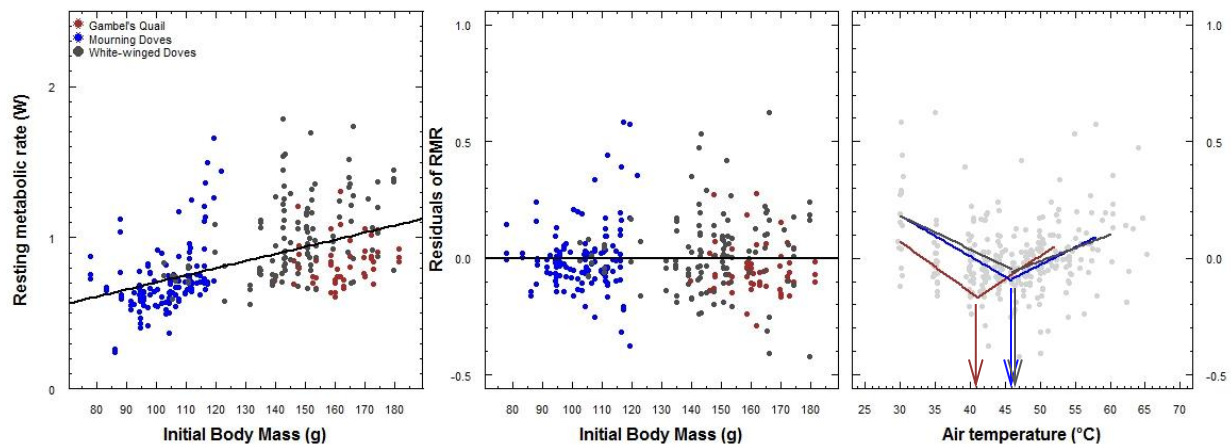


Fig. S1. The process of correcting resting metabolic rate (W) for body mass among the three species. 1) First we regressed RMR (W) against initial body mass (g), capturing the RMR residuals for each data point [left]; 2) then we regressed the RMR residuals against body mass to show that they successfully removed the effects of body mass on RMR [middle]; and 3) finally we regressed the RMR residuals against air temperature [right]. The graph on the right shows the segmented regressions of RMR residuals against air temperature for each species, along with the T_{uc} found from these regressions (41.1, 45.9, and 46.5°C for Gambel's Quail, Mourning Doves, and White-winged Doves respectively). See Table S1 for parameter estimates.

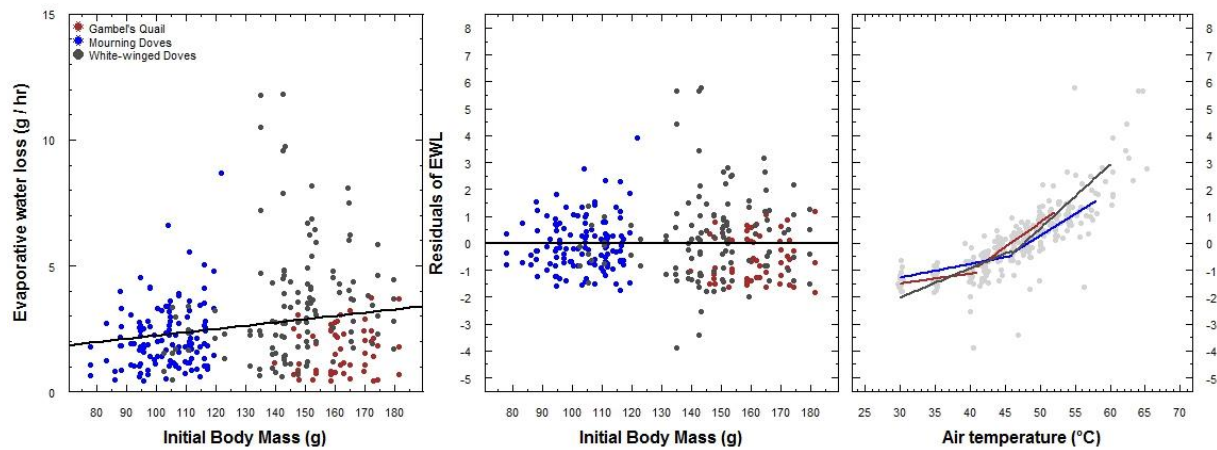


Fig. S2. The process of correcting evaporative water loss (g hr^{-1}) for body mass among the three species. 1) First we regressed EWL (g hr^{-1}) against body mass (g), capturing the EWL residuals for each data point [left]; 2) then we regressed the EWL residuals against body mass to show that they successfully removed the effects of body mass on EWL [middle]; and 3) finally we regressed the EWL residuals against air temperature above and below the T_{uc} [right]. See text for determination of T_{uc} using RMR residuals and Table S1 for parameter estimates.

Table S1. Slope (m) and intercept (b) for the relationship of mass independent residuals of resting metabolic rate (RMRr) and evaporative water loss rate (EWLr) in response to air temperature below and above the upper critical temperature (T_{uc}) in Gambel's Quail, Mourning Doves, and White-winged Doves.

Species	T_{uc}	regression	m	b	regression	m	b
Gambel's Quail	41.09	RMRr ($\leq T_{uc}$)	-0.022 (-0.031 -0.012)	0.72 (0.37 1.07)	RMRr ($> T_{uc}$)	0.020 (0.012 0.028)	-0.99 (-1.35 -0.63)
Mourning Dove	45.87	RMRr ($\leq T_{uc}$)	-0.018 (-0.027 -0.008)	0.71 (0.33 1.09)	RMRr ($> T_{uc}$)	0.015 (0.009 0.021)	-0.78 (-1.10 -0.45)
White-winged Dove	46.47	RMRr ($\leq T_{uc}$)	-0.013 (-0.021 -0.005)	0.55 (0.22 0.88)	RMRr ($> T_{uc}$)	0.011 (0.002 0.020)	-0.58 (-1.05 -0.11)
Gambel's Quail	41.09	EWLr ($\leq T_{uc}$)	0.036 (0.020 0.051)	-2.61 (-3.16 -2.06)	EWLr ($> T_{uc}$)	0.195 (0.168 0.222)	-8.93 (-10.22 -7.65)
Mourning Dove	45.87	EWLr ($\leq T_{uc}$)	0.061 (0.043 0.080)	-3.32 (-4.09 -2.56)	EWLr ($> T_{uc}$)	0.177 (0.155 0.199)	-8.52 (-9.69 -7.35)
White-winged Dove	46.47	EWLr ($\leq T_{uc}$)	0.137 (0.108 0.166)	-6.52 (-7.72 -5.32)	EWLr ($> T_{uc}$)	0.295 (0.237 0.353)	-14.19 (-17.22 -11.16)

Note: Values are means, with 95% confidence intervals in parentheses.

Table S2. Mean values and \pm SD for resting metabolic rate (RMR), rate of evaporative water loss (EWL), evaporative cooling capacity (EHL/MHP), and body temperature (T_b) in Gambel's Quail, Mourning Doves, and White-winged Doves at all air temperatures ($T_{air} \pm 1^\circ\text{C}$).

Gambel's Quail										
T_{air} ($^\circ\text{C}$)	30 $^\circ\text{C}$ (n=8)	35 $^\circ\text{C}$ (n=8)	40 $^\circ\text{C}$ (n=7)	42 $^\circ\text{C}$ (n=6)	44 $^\circ\text{C}$ (n=4)	46 $^\circ\text{C}$ (n=6)	48 $^\circ\text{C}$ (n=7)	50 $^\circ\text{C}$ (n=6)	52 $^\circ\text{C}$ (n=1)	
RMR (W)	1.01 \pm 0.18	0.78 \pm 0.08	0.75 \pm 0.08	0.75 \pm 0.10	0.78 \pm 0.02	0.79 \pm 0.11	0.79 \pm 0.09	0.94 \pm 0.11	1.06 \pm NA	
RMR (mW g $^{-1}$)	6.33 \pm 1.22	4.77 \pm 0.58	4.86 \pm 0.60	4.50 \pm 0.46	4.74 \pm 0.46	4.81 \pm 0.58	5.00 \pm 0.54	5.75 \pm 0.59	6.70 \pm NA	
EWL (g H $_2$ O hr $^{-1}$)	0.68 \pm 0.25	0.67 \pm 0.15	1.03 \pm 0.28	1.71 \pm 0.37	2.02 \pm 0.43	2.32 \pm 0.32	2.46 \pm 0.37	3.21 \pm 0.47	2.69 \pm NA	
EWL (% of Mb hr $^{-1}$)	0.43 \pm 0.15	0.42 \pm 0.09	0.67 \pm 0.16	1.03 \pm 0.22	1.23 \pm 0.30	1.42 \pm 0.23	1.57 \pm 0.25	1.95 \pm 0.21	1.70 \pm NA	
EHL/MHP	0.42 \pm 0.12	0.55 \pm 0.11	0.87 \pm 0.23	1.42 \pm 0.22	1.63 \pm 0.36	1.88 \pm 0.40	1.97 \pm 0.31	2.14 \pm 0.30	1.59 \pm NA	
T_b ($^\circ\text{C}$)	41.1 \pm 0.5	41.1 \pm 0.6	41.8 \pm 0.5	41.8 \pm 0.6	42.0 \pm 0.3	42.1 \pm 0.8	42.5 \pm 0.8	43.6 \pm 0.8	43.6 \pm NA	

Mourning Doves																
T_{air} ($^\circ\text{C}$)	30 $^\circ\text{C}$ (n=4)	35 $^\circ\text{C}$ (n=7)	40 $^\circ\text{C}$ (n=14)	42 $^\circ\text{C}$ (n=19)	44 $^\circ\text{C}$ (n=13)	46 $^\circ\text{C}$ (n=9)	48 $^\circ\text{C}$ (n=12)	50 $^\circ\text{C}$ (n=12)	52 $^\circ\text{C}$ (n=10)	54 $^\circ\text{C}$ (n=10)	56 $^\circ\text{C}$ (n=6)	58 $^\circ\text{C}$ (n=4)	60 $^\circ\text{C}$ (n=4)	62 $^\circ\text{C}$ (n=0)	64 $^\circ\text{C}$ (n=1)	66 $^\circ\text{C}$ (n=1)
RMR (W)	1.03 \pm 0.42	0.75 \pm 0.22	0.76 \pm 0.22	0.64 \pm 0.18	0.72 \pm 0.16	0.66 \pm 0.10	0.58 \pm 0.14	0.70 \pm 0.20	0.77 \pm 0.20	0.64 \pm 0.07	0.77 \pm 0.13	0.87 \pm 0.53	1.00 \pm 0.39	NA	0.90 \pm NA	0.75 \pm NA
RMR (mW g $^{-1}$)	9.41 \pm 3.16	7.37 \pm 2.32	7.07 \pm 1.67	6.32 \pm 1.71	7.01 \pm 1.98	6.07 \pm 0.72	6.11 \pm 1.72	6.72 \pm 1.64	7.94 \pm 2.04	6.14 \pm 0.56	7.39 \pm 1.22	8.28 \pm 3.80	8.92 \pm 2.65	NA	8.12 \pm NA	7.25 \pm NA
EWL (g H $_2$ O hr $^{-1}$)	0.71 \pm 0.28	0.74 \pm 0.16	1.29 \pm 0.49	1.27 \pm 0.44	1.69 \pm 0.32	1.91 \pm 0.21	1.96 \pm 0.42	2.45 \pm 0.39	3.00 \pm 0.55	3.10 \pm 0.39	3.73 \pm 0.46	4.01 \pm 0.75	5.52 \pm 2.17	NA	5.57 \pm NA	6.61 \pm NA
EWL (% of Mb hr $^{-1}$)	0.65 \pm 0.20	0.72 \pm 0.12	1.20 \pm 0.40	1.24 \pm 0.36	1.64 \pm 0.30	1.76 \pm 0.17	2.05 \pm 0.40	2.37 \pm 0.32	3.09 \pm 0.63	2.99 \pm 0.29	3.58 \pm 0.53	3.96 \pm 0.63	4.96 \pm 1.54	NA	5.02 \pm NA	6.37 \pm NA
EHL/MHP	0.44 \pm 0.04	0.65 \pm 0.19	1.05 \pm 0.17	1.26 \pm 0.25	1.51 \pm 0.29	1.83 \pm 0.17	2.19 \pm 0.47	2.27 \pm 0.35	2.47 \pm 0.23	3.08 \pm 0.43	3.08 \pm 0.48	3.37 \pm 1.27	3.54 \pm 0.66	NA	3.88 \pm NA	5.52 \pm NA
T_b ($^\circ\text{C}$)	41.0 \pm 0.1	41.0 \pm 0.7	41.7 \pm 0.5	42.0 \pm 0.5	42.1 \pm 0.7	42.2 \pm 0.5	42.1 \pm 0.8	42.1 \pm 0.8	42.9 \pm 0.9	42.2 \pm 0.8	41.9 \pm 0.9	42.0 \pm 1.1	43.1 \pm 1.3	NA	42.6 \pm NA	43.2 \pm NA

White-winged Doves																
T_{air} ($^\circ\text{C}$)	30 $^\circ\text{C}$ (n=3)	35 $^\circ\text{C}$ (n=8)	40 $^\circ\text{C}$ (n=12)	42 $^\circ\text{C}$ (n=12)	44 $^\circ\text{C}$ (n=13)	46 $^\circ\text{C}$ (n=11)	48 $^\circ\text{C}$ (n=15)	50 $^\circ\text{C}$ (n=10)	52 $^\circ\text{C}$ (n=10)	54 $^\circ\text{C}$ (n=7)	56 $^\circ\text{C}$ (n=5)	58 $^\circ\text{C}$ (n=5)	60 $^\circ\text{C}$ (n=2)	62 $^\circ\text{C}$ (n=3)	64 $^\circ\text{C}$ (n=2)	66 $^\circ\text{C}$ (n=0)
RMR (W)	1.22 \pm 0.10	0.98 \pm 0.39	0.93 \pm 0.25	0.99 \pm 0.25	0.86 \pm 0.20	0.91 \pm 0.22	0.97 \pm 0.28	0.93 \pm 0.21	1.07 \pm 0.24	1.01 \pm 0.31	1.05 \pm 0.13	1.17 \pm 0.25	1.37 \pm 0.24	1.04 \pm 0.36	1.45 \pm 0.47	NA
RMR (mW g $^{-1}$)	8.49 \pm 0.87	6.90 \pm 1.81	6.36 \pm 1.39	6.76 \pm 1.54	6.13 \pm 0.94	6.41 \pm 1.24	6.57 \pm 1.70	6.41 \pm 1.22	7.00 \pm 1.37	6.71 \pm 2.08	7.09 \pm 1.08	7.70 \pm 1.30	9.37 \pm 2.05	7.09 \pm 2.67	10.42 \pm 3.01	NA
EWL (g H $_2$ O hr $^{-1}$)	0.87 \pm 0.20	0.99 \pm 0.49	1.75 \pm 0.81	1.95 \pm 0.72	2.30 \pm 0.53	2.86 \pm 0.62	3.41 \pm 0.85	4.01 \pm 0.90	4.49 \pm 1.24	5.47 \pm 2.26	5.15 \pm 0.88	6.59 \pm 1.21	7.29 \pm 0.81	9.40 \pm 1.22	11.79 \pm 0.02	NA
EWL (% of Mb hr $^{-1}$)	0.60 \pm 0.14	0.69 \pm 0.23	1.20 \pm 0.48	1.32 \pm 0.47	1.63 \pm 0.28	2.01 \pm 0.29	2.31 \pm 0.51	2.76 \pm 0.51	2.95 \pm 0.77	3.64 \pm 1.55	3.47 \pm 0.52	4.39 \pm 0.95	4.99 \pm 0.75	6.49 \pm 1.45	8.52 \pm 0.31	NA
EHL/MHP	0.45 \pm 0.08	0.62 \pm 0.12	1.16 \pm 0.25	1.22 \pm 0.28	1.70 \pm 0.34	2.04 \pm 0.50	2.27 \pm 0.47	2.72 \pm 0.30	2.68 \pm 0.57	3.32 \pm 0.32	3.14 \pm 0.74	3.69 \pm 1.24	3.37 \pm 0.23	6.17 \pm 2.33	5.38 \pm 1.74	NA
T_b ($^\circ\text{C}$)	41.6 \pm 0.6	41.3 \pm 0.6	41.6 \pm 0.7	41.9 \pm 0.7	41.7 \pm 0.7	41.8 \pm 0.8	41.7 \pm 0.9	42.4 \pm 0.9	41.8 \pm 1.0	42.4 \pm 0.6	42.8 \pm 1.0	42.7 \pm 0.9	43.5 \pm 1.6	42.8 \pm 1.5	42.3 \pm 1.3	NA